

UNIFYING VESTIBULO-OCULAR REFLEXES

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Abstract – We present an eye/head gaze controller based on recent findings in biological gaze control. Despite the absence of an explicit VOR mechanism the model is able to (i) produce classical VOR responses and (ii) reject head perturbations during the saccadic portion of a gaze shift executed to a remembered target – what is usually attributed to a separate vestibular mechanism. We argue that distinguishing between both types of responses is not justified, as each is a manifestation of one reflex system having different goals during the stages of gaze redirection.

Keywords – VOR, vestibular, eye, head, gaze, oculomotor

I. INTRODUCTION

A reflex is a short-latency, involuntary response to a sensory stimulus. In principle, it helps a system continue to perform a given task in the presence of unexpected perturbations. The intrinsic reflex of the oculomotor system is known as the vestibulo-ocular reflex (VOR). It is classically defined as the counter-rotation of the eyes by the amount of head rotation, as sensed by the vestibular system, during the task of fixating a target. By this mechanism head motion is cancelled out by the resulting eye movement so that gaze in space remains on target (Fig. 1). In general, the VOR also helps preserve slow-phase gaze trajectories such as during target pursuit.

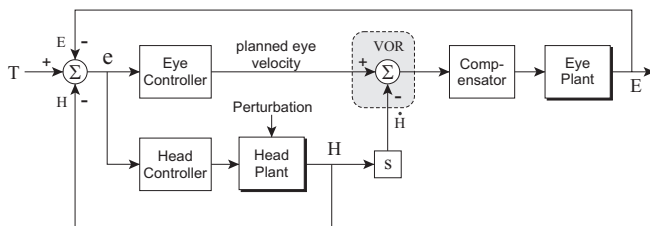


Fig. 1. A popular method of implementing the classical VOR mechanism within a gaze system. T, target angular rotation in space; E, eye angular rotation relative to head; H, head angular rotation relative to space. Note the 'VOR box' that explicitly implements a compensation scheme by subtracting head velocity from (planned) eye velocity.

Fig. 2 illustrates a gaze shift in which the eyes and head contribute to the trajectory. Note that the VOR definition treats head movement as an unwanted artifact that is first added to eye position in space (because the head carries the eyes) and then is subtracted out by the reflex. As a consequence of this, a gaze trajectory is expected to be invariant irrespective of whether or not the head moves. However, for large gaze shifts ($> 50^\circ$, in man) this hypothesis is violated and it is classically believed that the VOR is off during the eye saccade and becomes active again when the visual axis is stabilized in space [2].

Despite the evidence that the VOR is off during the saccadic portion of a gaze shift, vestibular information is not ignored during this segment. This is demonstrated in instances where gaze shifts are done in the dark to remembered targets in the presence of head perturbations (Fig. 3). Note that although the

saccadic portion of the gaze trajectory is not preserved in the presence of perturbations, in general, the accuracy of gaze shifts under such trying conditions is remarkable [3]. Since vision could not assist in correcting for perturbations in the gaze trajectory, compensation could only be possible through the use of vestibular information. As such, it is classically believed that since the VOR is off or attenuated during saccades that another vestibular mechanism (VM) acts to achieve accurate gaze shifts.

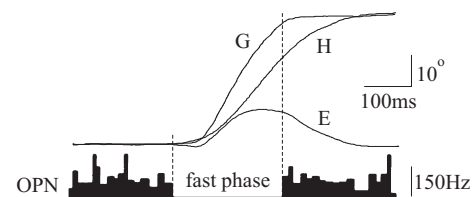


Fig. 2. Example of a single-step, 40° , horizontal gaze shift using eye-head movements in a cat. E, eye angular rotation relative to the head. H and G, head and gaze angular rotations relative to space, $G = E + H$. OPN, omnipause neuron activity that gates slow and rapid movement. Morphologically, the gaze shift may be decomposed into two stages consisting of an initial fast, or saccadic phase (OPN silent) followed by a slow-phase, or fixation segment. The slow-phase portion begins approximately when the gaze stabilizes in space near peak eye position. (Adapted from [2], Fig. 6C.)

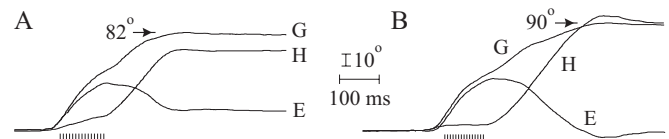


Fig. 3. Examples of the effect of unexpectedly restricting head motion while a human subject redirects gaze in the dark to a remembered target (flashed at 80° for 100ms). Striped bar under each graph indicates period over which a brake unexpectedly interrupted head motion. In both cases the brake occurred early in the head's motion. In A braking considerably slowed down the head. In B braking immobilized the head. Arrows indicate peak gaze overshoot. (Adapted from [3], Fig. 6 B & C.)

The assumption that two, distinct, vestibular mechanisms are necessary to account for the above observations is prejudiced by two factors: (i) classical black-box modeling of the oculomotor control system with its extension to gaze control, and (ii) failure to distinguish the difference between the presence of a sensory reflex and its definition.

With regard to modeling, anatomical and physiological findings of biological gaze systems support an integrated approach to gaze control. One ramification of this is that classical VOR functionality can be achieved without explicitly implementing a VOR 'box'. Furthermore, distributed connectivity allows one to implement the apparent separate vestibular mechanism required to model perturbed gaze shifts in the dark.

We will present a gaze controller with the above features. The ability to formulate a model void of an explicit VOR box

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suggests that the contemporary definition of this reflex be re-examined. Conceptually, the VOR is an ocular reflex evoked by vestibular stimulation. For that matter, the VM may be described in the same way. Recall the definition of a reflex at the start of this paper and note that the VM helps the gaze system perform a given task (the redirection of gaze) in the presence of unexpected perturbations. Hence, the VM, too, is a reflex; acting toward the same goal as the VOR but distinguished merely by the task that it assists. By defining the VOR with respect to context (i.e., defining it as the effect of the vestibular system on a task) then both classical VOR and VM may be unified as one phenomenon.

II. METHODOLOGY

A. Features of the gaze controller

Fig. 4 shows the block diagram of the gaze controller used in this paper. Its aspects have been described in [2] and [8] and only salient points will be summarized here.

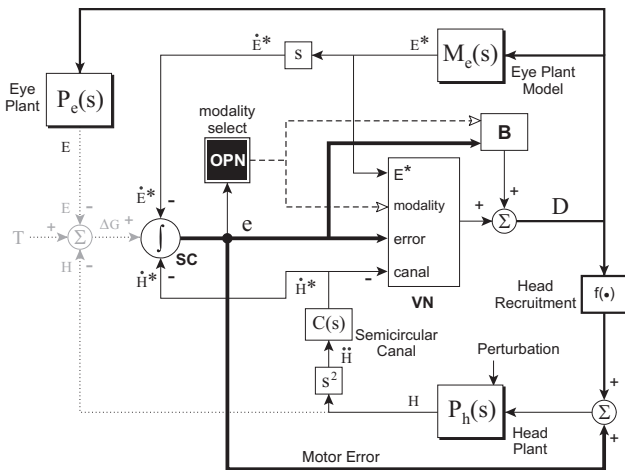


Fig. 4. Block diagram of the gaze controller. Dotted pathways represent visual feedback (disabled in this paper). Gains along branches have been omitted to improve readability. New symbol definitions: ΔG gaze error; T target in space; **SC** superior colliculus, integrating the sum of inputs; **VN** vestibular nucleus, a summing node with selectable pre- and post-summing gains; **B** burster neurons, active only during fast-phase; e motor error; D pre-motor drive; * superscript indicates efferent estimate; a dot above a variable indicates a time derivative. The perturbation input is a velocity input. A gaze shift to a remembered target is elicited by imposing an initial condition on the **SC** integrator and proceeding with the simulation.

When published, in 1992, the model represented the first concerted effort of synthesizing a gaze controller that incorporated recent physiological findings in biological gaze control. Yet, it was based on two assumptions that needed reconciliation. The first assumption, that the eye and head shared a common pre-motor drive, was upheld in 1996 with the discovery of (secondary) vestibulo-spinal neurons that carried eye movement-related signals [1]. The second assumption, that the superior colliculus (SC) was involved in coordinating slow-phase eye movements (its role in saccadic movements was already established), was confirmed in 1997 with the report that the output of the SC encoded an error signal that was updated for both slow and rapid eye movements [4]. Thus, at present, the

proposed controller topology remains unchallenged. With this in mind, we now summarize its key features.

- Dual-modality control, slow and fast phases, is achieved by parameter switching. The OPN determines the appropriate operating modality based on the motor error.
- The model makes extensive use of distributed signals. Vestibular information is distributed to two levels, the SC and VN. Motor error is distributed to three levels, the VN, B, and the head. And, finally, the pre-motor drive is distributed to two levels, the eye and head.
- Since the output of a semicircular canal is high-pass-filtered head velocity, sensory information passing via the SC integrator becomes band-limited, whereas that passing through the VN retains its high-frequency content. Hence, one branch of the controller is suitable for low-frequency operation and the other for high-frequency operation.
- Vestibular information is used by way of negative feedback. During the fast-phase modality the VN canal input is ignored (internally set to zero).
- Servoing (without vision) is done exclusively on internal estimates of eye and head states.

B. Measuring the VOR gain

A popular method in the literature for measuring (head-free) VOR gain is to evaluate the instantaneous ratio of eye and head velocities. Though convenient as a method the result obtained is not related to VOR gain. We shall illustrate this using a traditional example and support an alternate method for estimating the gain, in general, at high frequencies.

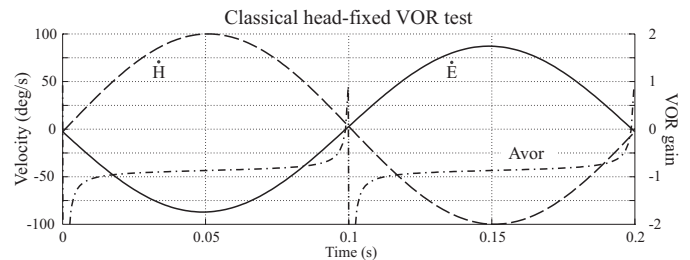


Fig. 5. Illustration of the classical vestibulo-ocular reflex. (Idealized simulation.) VOR gain is -0.87 . In these experiments head velocity, \dot{H} , is made to vary in a sinusoidal manner which produces the resulting eye velocity profile, \dot{E} , in steady state. It is worth noting that \dot{H} is an independent variable and \dot{E} is dependent. In principle, $\dot{E}(s)/\dot{H}(s)$ is a high-pass transfer function. $A_{\text{vor}} = \dot{E}/\dot{H}$ is the instantaneous VOR gain. See text.

Fig. 5 shows the traditional head-fixed VOR. Given such an input-output pair, the VOR gain is almost universally evaluated as (Amplitude of \dot{E})/(Amplitude of \dot{H}). This is perfectly fine, as \dot{E} is the steady-state response of a linear system to a sinusoidal input, and the gain of a transfer function at a given frequency is defined precisely in this way. A_{vor} is a function of time that attains ridiculous values. Clearly, A_{vor} is a useless measure as far as VOR gain is concerned. Yet, inexplicably, it is often used to gauge VOR gain during head-free gaze shifts. The problem does not end here, however.

During head-free gaze shifts directed towards a target, eye and head movements are correlated. That is, \dot{H} is no longer an independent variable and \dot{E} is no longer its dependent result; the independent variable is the gaze input that elicited the gaze shift. Under these conditions, all means of evaluating VOR gain by comparing eye and head trajectories produce biased results (especially the ill fated Avor method). In order to perform valid analyses, it is necessary to de-correlate eye-head movements [5].

One approach is to momentarily perturb the head during the course of the elicited gaze shift and analyze the perturbations in the eye-head trajectories. Under the assumption of linearity, both eye and head trajectories will comprise a base-line response, elicited by the gaze input, superimposed with a perturbation component. Since the head perturbation is uncorrelated with the gaze input the base-line component may be de-trended from the composite eye and head trajectories leaving the perturbation components. With respect to the perturbation components, \dot{H} is an independent input and \dot{E} is its dependent output, which are appropriate conditions for an un-biased analysis.

In practice, the duration of perturbations is short. As such, this technique is useful mainly for probing systems at high frequencies. In a lab setting braking and tapping the head are two examples of suitable perturbations (e.g., [3, 7]).

III. RESULTS

Simulations have been carried out using MATLAB and SIMULINK¹. In all figures, *solid black bars* under the horizontal axis indicate a fast-modality segment; *striped bars* indicate periods when head perturbations were applied. Note that only one parameter set has been used in all simulations and that the controller selected the operating modalities automatically.

The model produced classical VOR gain having a range of $[-0.90, -0.77]$. Results were obtained using sinusoidal perturbations after nullifying the ‘active’ head drive. Tests were performed at three target values, 0° , 60° , and 120° , with perturbation frequencies ranging from 1 to 20Hz and amplitudes 10 and 400 deg/s. VOR gain values are comparable with published physiological data.

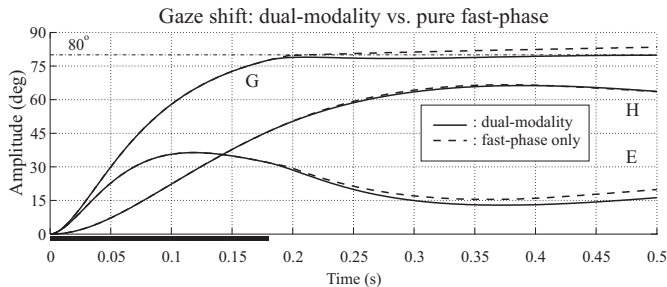


Fig. 6. Resulting gaze trajectories when the controller is restricted to operate in fast modality (*dashed lines*) and when free to select between slow and fast modalities (*solid lines*).

Fig. 6 compares gaze trajectories when the controller is frozen in fast-phase modality to those of when it is allowed to operate

normally. Note the minor differences between both cases following the fast-phase segment. Even more striking is that the eye can reverse direction during the fast-phase modality (note two reversals of dashed line²). Evidently, gaze trajectory alone does not reveal the extent of the saccadic portion of a gaze shift.

Fig. 7 shows an example of a gaze shift performed to a remembered target while the head is momentarily perturbed at two instances in time. The first perturbation occurs during the saccadic portion of the gaze shift, when the classical VOR is said to be off. Gaze gets on target nonetheless, and does so sooner since the perturbation accelerated the head in the direction of original motion. The second perturbation occurs during the fixation segment, where classical VOR is defined. The measured VOR gain from perturbed components is -0.89 .

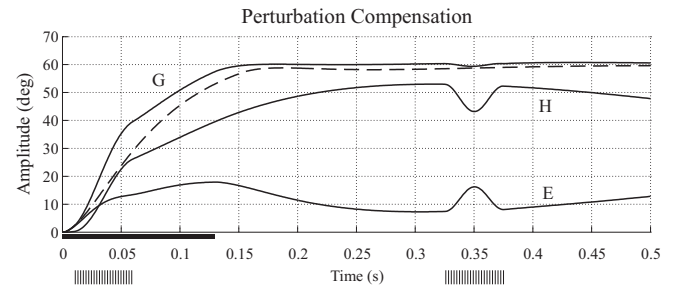


Fig. 7. Controller response when executing a 60° gaze shift, to a remembered target, in the presence of head perturbations. For reference, the dashed line shows the gaze trajectory when perturbations are absent. The perturbation profile is a sinusoid, $\Delta H = 600 \sin(20\pi t)$ deg/s, gated to isolate portions of cycles. In the first perturbation, the head is accelerated with half a cycle. In the second one, the head is decelerated then accelerated over a full cycle.

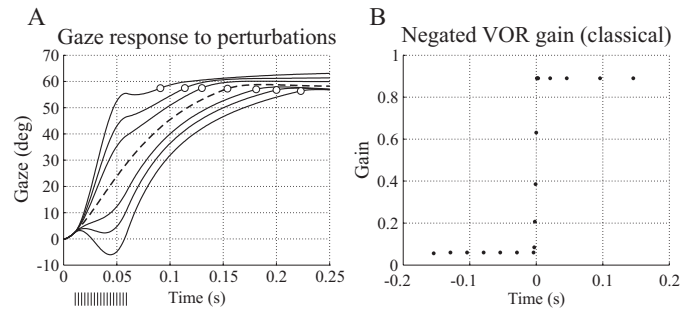


Fig. 8. Examples of vestibular reflexes. In A, gaze end-point performance for 60° gaze shifts in the presence of various perturbations. The reference trajectory (*dashed line*) was obtained in the absence of perturbations. Circles indicate the end of the fast-phase segments, where the OPN determined that the gaze reached its target. The perturbation profile is half a cycle of a 10Hz sinusoid. Starting from the reference curve and moving outwards, the perturbation amplitudes are 600, 1000, and 1500 deg/s. Curves below the reference had perturbations applied opposite to original head motion; those above the reference had perturbations applied in line with original head motion. In B, VOR gain measured during various stages of a 60° gaze shift using perturbation analysis. Single perturbation ‘blips’ were applied at various times prior to and following the modality transition, at 0s. (I.e., the end-times of the saccadic portion of the gaze shifts are normalized to 0s.) Perturbation blips consisted of a full cycle of a 50Hz sinusoid with amplitude 10 deg/s.

Fig. 8 illustrates the performance of the vestibulo-ocular reflexes. Panel A illustrates that gaze end-points are robust in the presence of large perturbations (small vertical spread of circles).

¹ Both available at <http://www.mathworks.com>

² The reversal at around 355ms is due to the use of a 2nd-order eye plant.

Hence, the vestibular reflex in this context is functioning well. As expected, gaze shifts take longer to execute when perturbations decelerate the head and terminate sooner when the perturbations accelerate the head toward the goal. Panel B shows measured classical VOR gains, confirming that during the saccadic portion of a gaze shift ($t < 0$) the gain is heavily attenuated. However, as expected, during the fixation segment ($t > 0$) the gain is high. Narrow perturbations were used in order to allow probing of the VOR gain with a high resolution.

IV. DISCUSSION

In much of oculomotor literature, there is an apparent shared ideology that treats the (classical) VOR as a selectable task operating within a gaze control system. This would explain why many models implement the VOR function by explicitly subtracting head velocity from eye velocity. However, the manifestation of a sensory reflex bears no evidence as to its manner of implementation. Hence, the modeling problem is open to many alternatives. The model presented in this paper illustrates a different means of achieving vestibular reflexes as observed in biological systems.

In Fig. 4 there is a distinct lack of a VOR compensation mechanism, a ‘VOR block’ where \dot{H} would be subtracted from \dot{E} . Vestibular information is incorporated within the controller through two negative feedback loops. The loop through SC implements position control, whereas the loop through VN implements velocity control. Conceptually, both pathways correct the gaze trajectory by adjusting the goal by the amount of sensed head perturbation. Also, by virtue of the architecture, the controller inherently distinguishes between self-generated and externally induced sensory events.

During slow-phase segments, vestibular projections to SC and VN are active. As a result of the various elements in the model, position control works effectively at low frequencies, whereas velocity control works better for high frequencies. Hence the system is able to respond to high-frequency perturbations as in the classical VOR case. During fast-phase segments the VN projection is lost and the system is transformed into a high-bandwidth position controller (by gain adjustments). Hence, akin to the vestibular mechanism mentioned in the introduction, saccadic goals are preserved in the presence of perturbations while the classical VOR is deficient.

Eye trajectory reversals are not necessarily due to classical VOR effects. As demonstrated in Fig. 8B, classical VOR is heavily attenuated during the saccadic portion of a gaze shift. Yet significant eye reversals can occur during such segments. (See Fig. 6.) Such behavior can be accounted for solely by having the eye and head plants form feedback loops driven by a shared motor drive³. Hence, the shared coordination of plants works synergistically with the vestibular system.

Despite the rapid turn-on of the classical VOR near the end of the saccadic portion of a gaze shift (Fig. 8B), the VOR appears to be modulated more gradually in biological systems (e.g., [6]). One factor that could account for this is that, in our model, parameters change values between the two operating modalities within one millisecond. Biological systems cannot respond so rapidly. This is an area for future development.

V. CONCLUSION

Throughout this paper, we have maintained the distinction between the so-called VOR and VM for the sake of keeping in-step with contemporary nomenclature. However, in the presented model neither mechanism exists as an entity – though the reflexive response associated with each may be elicited. Hence, the distinction made between both mechanisms is a misleading fabrication, and is totally unnecessary.

Vestibular information is used at every instance of gaze coordination. Globally, it helps the gaze system perform a task in the presence of head perturbations. The type of vestibular response may be different depending on the goal that the gaze system strives to achieve, but the intent is universal: the rejection of head perturbations.

Hence, the term “VOR” should be recognized as the general term it really is: the reflexive response of the oculomotor system due to a vestibular sensory stimulus.

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³ Skeptics can illustrate this to themselves by considering a position feedback system in which gaze error is fed to both eye and head plants, and where the gaze is compared against a reference gaze signal. As in nature, one plant (the eye) needs to be faster than the other (the head) for a good effect.